FORAGING BEHAVIOUR OF CARPENTER BEES, GENUS *XYLOCOPA* : XYLOCOPIDAE : HYMENOPTERA, AND THE POLLINATION OF SOME INDIAN PLANTS[1]

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Key words: Foraging behaviour, pollination, carpenter bees, *Xylocopa latipes, X. pubescens*

Carpenter bees, or species of *Xylocopa,* are prominent members of the Indian bee fauna. They are found throughout the year, foraging in daylight and rarely through the moonlit hours. Some plant species are adapted specifically to pollination mediated by nectar-seeking carpenter bees. Such flowers protect the nectar chamber against piercing. Some offer pollen from poricidal anthers as the only reward. By their flower-foraging behaviour, carpenter bees provide an excellent service to the plants that they pollinate, especially obligate outcrossers like *Gmelina* and *Cochlospermum.* The different types of foraging behaviour exhibited and the role played by carpenter bees in the pollination of various plant species occurring in Visakhapatnam, Coringa and Giddalur in Andhra Pradesh are discussed.

INTRODUCTION

Large carpenter bees of the cosmopolitan genus *Xylocopa* (Family Xylocopidae, Hymenoptera) are the most prominent members of the Indian bee fauna. They are usually black on the abdomen and variously coloured in the thoracic region. They nest in soft dead wood of various plant species. Male and female vary in size, and generally both have long tongues. They feed on the flowers of various plant species blooming at different times of the year. Their foraging activity is usually limited to daylight hours, but some extend their activity into moonlit hours as well (Maxwell-Lefroy and Howlett 1971). The male carpenter bees collect only nectar, while the females gather pollen and nectar to provision brood cells. Both have a high energy expenditure when foraging (Chappel 1982) due to their large mass, and this expenditure must be balanced by energy obtained from nectar sugar.

The bees can carry quantities of nectar and pollen that are large, relative to the amounts usually available in flowers, and thus they visit many flowers or plants during a foraging trip. While probing the flowers for pollen or nectar, the bees usually contact stigmas and anthers, and thereby pollinate flowers. Some plant species with obligate outcrossing ability are exclusively pollinated by carpenter bees, while some others with self- and outcrossing ability are also pollinated by other insects. Further, there are mutualistic pollinating relationships between carpenter bees and plants (Snow and Roubik 1987, Scott *et al.* 1993). The carpenter bees exhibit various flower-foraging behaviours such as opportunistic, territorial, traplining, buzzing, and others for utilising forage efficiently. These behaviour patterns benefit the plants largely in outcrossing. Altogether, the foraging of carpenter bees provide an excellent service for plants that they pollinate, especially for obligate outcrossers, and enhances the fecundity and adult maintenance in bees. In view of the importance of foraging behaviours of carpenter bees in pollination, this paper aims at describing the floral, structural and functional features of 15 plant species and their adaptations to pollination by carpenter bees *Xylocopa latipes* and *X. pubescens* (Table 1). Of these, two are mangrove plant species, *Acanthus ilicifolius* and *Caesalpinia nuga*, occurring in estuarine habitats of Coringa (16° 55' N, 82° 15' E). Two others, *Anisomeles malabarica* and *A. indica* are

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TABLE 1

DETAILS OF FLOWERS AND FORAGERS OF DIFFERENT PLANT SPECIES

Plant species	Flowering period	Flower opening	Anther dehiscence	Flower colour	Nectar volume (µl)	Nectar concentration (%)	Breeding system	Flower visitors	Forage collection	Foraging behaviours of carpenter bees
ACANTHACEAE										
Acanthus ilicifolius	May-Aug	Day-time	L	Bl	5.0	35-40	X, G	Cb, Sb	N	Te
ALANGIACEAE										
Alangium salvifolium	Feb-Apr	24-hours	L	Cr	0.8	25-29	X, G	B, Cb, W, F, Bu	N, P	Te, Tr
LAMIACEAE										
Anisomeles malabarica	Oct-Jan	0100-0500	L	Pu	1.8	30-48	X, G, A	B, Cb, W, An, Th, Bu, Sb	N, P	Te, Tr
A. indica	Oct-Jan	0530-0730	L	Pu	1.6	32-43	X, G, A	B, Cb, W, An, Th, Bu, Sb	N, P	Te, Tr
CAESALPINIACEAE										
Bauhinia purpurea	Oct-Jan	0430-0530	L	Pu	T	5-7	X, G, A	B, Cb, W, Bu,	N, P	Op
Caesalpinia nuga	Mar-Jan	0600-1000	L	Ye	T	-	X, G (?)	Cb	N	Tr
Cassia alata	Oct-Feb	0300-0400	P	Ye	-	-	X, G	Cb	P	Buz
Peltophorum pterocarpum	Mar-Jun	Forenoon	L	Ye	T	-	X, G	B, Cb	N, P	Buz
Tamarindus indica	Apr-Aug	2300-0400	L	Cr	1.0	6-8	X, G	B, Cb, An, W, F, Bu	N, P	Tr
COCHLOSPERMACEAE										
Cochlospermum religiosum	Jan-Apr	2300-2400	P	Ye	-	-	X, G	B, Cb	P	Buz
LECYTHIDACEAE										
Couroupita guianensis	Feb-Mar	0700	L	Ye	-	-	X	B, Cb	P	Op
FABACEAE										
Gliricidium sepium	Jan-Mar	0730-1600	L	La	3-4	34	X, G	B, Cb	N, P	Tr, Op
VERBENACEAE										
Gmelina aisatica	Mar-Oct	0500-0600	L	Ye	75-80	20-28	X, G, A	B, Cb	N, P	Tr
MARTYNIACEAE										
Martynia annua	Jul-Oct	0400-0500	L	Bl	15	5-7	X, G, A	B, Cb, H	N, P	Op
MORINGACEAE										
Moringa oleifera	Feb-May Sep-Nov	0500-0900	L	Wh	1.3	5-18	X, G	B, Cb, An, W, F, Bu	N, P	Tr, Op

L-Longitudinal, P-Poricidal, Ye-Yellow, Cr-Creamy-white, La-Lavendar, Bl-Blue, Pu-Purple, Wh-White; T-Traces, X-Xenogamy, G-Geitonogamy, A-Autogamy; B-Bees, Cb-Carpenter bees, F-Flies, W-Wasps, An-Ants. Th-Thrips, Bu-Butterflies, H-Hawkmoth, Sb-Sunbirds; N-Nectar, P-Pollen; Te-Territoriality, Tr-Traplining, Op-Opportunistic, Buz-Buzzing.

inhabitants of the foothills of Giddalur area (15° 10' N, 18° 45' E); all others occur in Visakhapatnam (17° 42' N, 82° 18' E).

The floral features and foraging behaviour of carpenter bees with reference to pollination have been reported by Aluri (1990, 1993); Aluri and Subba Reddi (1989, 1994, 1996a, b); Bhaskara Rao and Subba Reddi (1994a, b); Jyothi *et al.* (1990); Subba Reddi and Aluri (1997); Subba Reddi and Bhaskara Rao, (1993); and Subba Reddi *et al.* (1996, 1997). The foraging behaviour of carpenter bees and breeding systems have been further studied extensively in the field, where the abovementioned plant species occur.

Floral details and foraging behaviour of carpenter bees

1. ***Acanthus ilicifolius* L.** (Acanthaceae): This plant grows in the estuarine habitats of Coringa and adjoining areas in the Godavari delta and flowers during May-August. Its flowers are large, blue and nectariferous. The flower has a cartilaginous corolla tube, terminating in an upper lip sheltering stamens and the pistil, and a lower lip which serves as a landing site for foragers. The stigma projects beyond the anthers. The pollen receptacle consists of fertile and sterile anthers, which are firmly interlocked. Separation of these locules and subsequent liberation of pollen are possible only by large-bodied pollinators. The flowers are visited by carpenter bees along with sunbirds for nectar; both are equally efficient in exploiting the nectar and effecting cross-pollination. While probing the flower, the carpenter bee inserts its proboscis through the pollen receptacle with much force to get at the nectar. This results in the separation of fertile locules from the sterile ones and shedding pollen on to the back of the bee and on the stigma. If the bee carries pollen from the previously visited flower, it results in cross-pollination or else effects selfing. The separated anther locules regain their original position with the departure of the bee. In consequence, the flowers receive multiple visits, hence cross- or self-pollination is ensured. The bees show fidelity to this plant throughout its flowering by exhibiting territorial foraging behaviour to exploit the nectar.

2. ***Alangium salviifolium* (Linn. F.) Wang.** (Alangiaceae): A small deciduous tree, it sheds leaves before flowering. It flowers during February-April. Although the flowers are open day and night, they are foraged for pollen and/or nectar by diurnal insects — bees, wasps, flies and butterflies. Of these, carpenter bees show fidelity to this plant by foraging throughout the flowering period and largely effecting cross-pollination. The flowers stand out visually by their large display and by shedding leaves which attract the bees. The carpenter bees exhibit traplining and territorial foraging behaviour. Traplining is employed to forage on the distantly spaced plants intermingled with other plant species, and territoriality to forage on the plants aggregated in one place. These two behaviour patterns occur throughout the flowering period, and probably promote xenogamy.

3 & 4. ***Anisomeles malabarica* R. Br.** and ***A. indica* O. Kuntze** (Lamiaceae): These two species are herbaceous perennials and grow from both rootstock and seed. *A. malabarica* shows vegetative growth in July, flowers during mid-October and disappears in January. *A. indica* shows vegetative growth and flowers during October to mid-January. It exhibits flowering episodes in response to water stress. The flowers open from 0100-0500 hrs in *A. malabarica* and from 0530-0730 hrs in *A. indica*. The flower structure of the two species is similar. The flowers are purple, showy, large, fragrant, bisexual and nectariferous. They are bilabiate, with stamens and style extending beyond the small upper lip resembling the classical gullet type blossom. Day-flying bees, wasps, ants, thrips, butterflies and sunbirds visit the flowers of both species, of which only carpenter bees and sunbirds are regular and perform efficient and effective

pollination. Other foragers visit the flowers occasionally, and some of them deplete the floral forage by probing from the side of the flowers, bypassing the pollination apparatus. The carpenter bees, after landing on the strong lower lip, probe flowers in an upright position for nectar, during which the stigma situated near the tip of upper lip contacts the residual pollen in the dorsal crevice of the bees. The male carpenter bees exhibit territorial and traplining foraging behaviour and collect only nectar. This dual behaviour greatly profits the taxa in achieving outcrossing. Sunbirds are equally important for pollination. They feed on the nectar of flowering *Anisomeles* throughout winter.

5. ***Bauhinia purpurea*** **Linn.** (Caesalpiniaceae): An evergreen, popular ornamental tree, flowers during October-December; some trees may flower up to February. The flowers open daily from 0430-0530 hrs. They are large, purple, showy, bisexual and nectariferous. The flowers are dichogamous, showing anther dehiscence in 1st day flowers and stigmatic receptivity in 2nd day flowers. This floral trait precludes self-pollination. The availability of both phases in different flowers on the same plant on a day facilitates geitonogamy. The flowers are foraged by bees, wasps and butterflies; bees are regular, consistent foragers, while wasps and butterflies are occasional and least important in effecting pollination. Among bees, the carpenter bee and the digger bee *Amegilla,* are the principal pollinators. The carpenter bee usually alights on the staminal filaments and crawls into the flower, seeking nectar. While taking off, the bee's body touches the anthers and the pollen is deposited on the dorsum. If the bee, after its visit to a 1st day flower, visits a 2nd day flower, the receptive stigma contacts precisely with the pollen deposited area and results in pollination. They forage equally on male and female phase flowers, thereby promoting geitonogamy and xenogamy. Sometimes the bees probe the flowers laterally, bypassing the pollination apparatus, a behaviour pattern known as side-working. About 25% of the foraging visits relate to side working.

6. ***Caesalpinia nuga*** **Ait.** (Caesalpiniaceae): It thrives well in the estuarine habitats of Coringa and blooms during March-June. Its flowers are large, bisexual, protandrous and nectariferous, opening every morning. The flowers are aromatic, yellow with nectar guide on the upper petal, and the reproductive structures placed near the lower part of the corolla. *Xylocopa latipes* and *X. pubescens* are the principal pollinators; they are diurnal foragers and collect only nectar. Guided by the nectar guide, the bees probe the flower in upright position and contact anthers and stigma with their sternum. They exhibit traplining foraging behaviour.

7. ***Cassia alata*** **L.** (Caesalpiniaceae): It is a herbaceous shrub and blooms in October-February. The flowers open daily between 0300-0400 hrs. They are large, yellow, bisexual, nectarless and exhibit heteranthery, having feeding pollinating anthers with poricidal dehiscence, and enantiostyly having right and left stylar orientation. Carpenter bees are the exclusive foragers of this plant, collecting pollen by buzzing. While buzzing, the vibration of the bee causes discharge of pollen from the pollinating anthers on to the sides of the bee's thorax and abdomen. At the same time, the pollen grains are transferred to the stigmas oriented to the right or to the left. The intensity of buzzing increases with bee size, resulting in more effective pollen discharge and pollination. Heteranthery and enantiostyly, with the buzzing behaviour of pollinator carpenter bees promote cross-pollination.

8. ***Peltophorum pterocarpum*** **Backer ex. K. Heyne** (Caesalpiniaceae): Flowers profusely during March-June. The flowers open during daylight hours. The large, bright yellow corolla is a convenient landing site for the pollinator. Monomorphic anthers release pollen all at once,

along the entire length of the anthers, typically by complete longitudinal stomial slits, filiform style terminating in a capitate stigma lying above the stamens, and the nectar produced in traces is hidden by dense silky structures present at and around the basal parts of stamens. The flowers are promiscuous to any visitor species but carpenter bees, *Ceratina* and *Trigona* are the only foragers. Among the foraging bees, *Ceratina* and *Trigona* are small in size, and hence inappropriate for pollination. Further, they are infrequent visitors. The carpenter bees are large in size, regular and frequent foragers. They are the principal foragers, effecting pollination while probing for pollen and/or nectar. The male carpenter bees collect nectar and the females both nectar and pollen. Both sexes probe the flower legitimately for nectar. The pollen feeding females probe the flower by buzzing. After landing on the petals and/or stamens, they rapidly contract the indirect flight muscles, producing strong vibrations that are transmitted directly to the anthers, indicated by the audible buzzing of the bees. The vibrations rapidly produce a pollen cloud from the anthers, which along with the stigma, simultaneously strike the ventral side of the bee and result in sternotribic pollination. The buzzing is very brief at sunrise and gradually increases towards midday. Further, the floral vibrations are single buzzes in the morning hours, and the bees stay at one position on the flowers. Later in the day, the bees use multiple buzzes and rotate on the flowers, depending on the availability of pollen. This results in the most efficient extraction of pollen, promoting outcrossing.

9. ***Tamarindus indica* Linn.** (Caesalpiniaceae): A tall tree that has become indigenous, now commonly found in the tropics. It flowers from April to August. The small, creamy, bisexual, nectariferous flowers open each night between 2300-0400 hrs. The corolla is tubular at the base and has one small central petal rolled upwards, and two large lateral ones. The gynaecium exhibits enantiostyly. Although the flowers open at night, they are foraged by diurnal insects. The foragers include bees, ants, wasps, flies and butterflies. Of these, bees are dominant and among them, honey bees are the major pollinators while carpenter bees act as minor pollinators. Nectar gathering carpenter bees first land on the central petal in an upright position, and then insert into the tubular part of the corolla. This facilitates simultaneous contact of the sex organs with the bee's back, resulting in nototribic pollination. Although carpenter bees are minor pollinators, their inter-tree flight behaviour assumes great significance if cross-pollination of all the pollinator insects is considered.

10. ***Cochlospermum religiosum* (L.) Alston** (Cochlospermaceae): A deciduous, tropical tree, it is used commercially and for the afforestation of bare, rocky, denuded hills. After shedding leaves, it flowers during January-April. The large, showy, bright yellow, bisexual, nectarless flowers open daily from 2300-2400 hrs. The stamens are numerous and arranged in two whorls, anther dehiscence is poricidal. The style with a capitate stigma projects out from the base of the ovary and stands at the level of anthers. The flowers are foraged for pollen by carpenter bees *Xylocopa*, *Amegilla*, honey bees *Apis cerana indica, A. florea* and stingless bees *Trigona*; but only carpenter bees are regular, consistent and effective in harvesting the pollen crop. The others are occasional foragers, and play a minor role as pollinators. The carpenter bees, upon landing on the anthers, vibrate their body to discharge pollen through the apical pore of the anthers. The entire body of the carpenter bees is sprinkled with pollen, but most of the pollen is deposited on the ventral side of the bee. The pollen laden bees when foraging on the same or other inflorescences on the same plant effect geitonogamy and on flowers of different conspecific plants effect xenogamy.

11. ***Couroupita guianensis* Aubl.** (Lecythidaceae): Flowers almost throughout the

year with heavy flowering in February-March. It exhibits cauliflory. The flowers are inverted, yellow on the abaxial face and purple on the adaxial face, nectarless but produce abundant pollen. The androecium is characterized by stamens of the ring and hood which are connected by a stamen-free ligular structure. The ring stamens serve as pollinating stamina, and hood stamens as feeding stamina, exhibiting heteranthery. The stigma has a star-like fissure and becomes receptive after anther dehiscence. The flowers open daily around dawn. Their fragrance is released through osmophores present in the corolla and at the top of the filaments of the hood anthers. Carpenter bees, honey bees and the stingless bee are attracted to this fragrance. Considering their frequency, foraging behaviour, efficiency in harvesting pollen and effective pollination, carpenter bees assume principal pollinator status.

The carpenter bees, while entering the flower, push the hood down, causing the release of pollen (tetrads) that simultaneously adhere to the ventral part of the bee and are accessible for grooming. After entering the flower, they collect pollen from the hood, and during pollen collection they rub their dorsal parts against the ring anthers and the stigma, detaching several ring anthers in the process, resulting in nototribic pollination. The bees opportunistically visit the plant for pollen and other plants like *Gliricidia sepium* and *Peltophorum pterocarpum* for nectar during the same period.

12. ***Gliricidia sepium* (Jacq.) Walp** (Fabaceae): It is widely cultivated in the tropics for shade and as an ornamental tree. It sheds leaves before flowering and flowers from January to mid-March. Its flowers open between 0730-1600 hrs. The flowers are lavender, large, bisexual, odourless and nectariferous. The corolla is characteristically papilionaceous and has a light greenish-yellow glistening spot serving as a nectar guide. Stamens are diadelphous, and the style springs through the staminal tube and overarches the stamens. The flowers are visited by *Xylocopa* (Family Xylocopidae) *Trigona* (Apidae) and *Ceratina* (Anthophoridae). Xylocopid bees are large, abundant and regularly forage for nectar, while the other two bees are small, foraging occasionally for pollen and nectar. Their foraging behaviour, coupled with floral features such as spacious, strong corolla, light colour, and nectar hidden by the staminal tube, indicate that carpenter bees are the principal pollinators, while the other bees are incidental pollinators. Carpenter bees forage in sunlight. They probe the flowers in upright position and make regular contact with stamens and stigma sternotribically. The flowering trees stand out visually and appear conspicuous to the bees from a distance because of their large floral display, which enables the carpenter bees to exhibit traplining. Towards the end of the flowering period, floral density is reduced, compelling the carpenter bees to forage opportunistically on this taxon and on the nearby *Peltophorum pterocarpum* for pollen and/or nectar, and *Cassia* species for pollen, which is available at the same time.

13. ***Gmelina asiatica* Linn.** (Verbenaceae): A deciduous, perennial, straggling shrub, flowering from March-October. The flowers open between 0500-0600 hrs every day. They are large, yellow, bisexual and nectariferous. The corolla is tubular at the base and its free end is inflated into a bilipped bell-like structure with the upper lip enlarged and the lower lip with a large central lobe and two small lateral lobes. Stamens are didynamous and epipetalous. The stigma is simple and stretched beyond the anthers. The flowers are foraged exclusively by day-foraging bees, e.g. *Xylocopa*, *Amegilla*, *Trigona* and *Ceratina*. Effective pollination in this shrub is by carpenter bees, which forage for nectar only. They approach the flower in upright position, land on the lower corolla lip and crawl into the tubular part, stretching their proboscis to full length. In doing so, the dorsal surface of their

body makes initial contact with the stigma and then with the dehisced anthers, effecting nototriby. If the bees carry on their back conspecific pollen from previously foraged flowers, they effect cross-pollination by their initial contact with the stigma. The other bees are of no use to the plant as pollinators, but nectar depletion by *Amegilla* indirectly forces carpenter bees to pay multiple visits to the flowers to satisfy their energy requirement. Further, the carpenter bees exhibit traplining, which promotes cross-pollination.

14. ***Martynia annua* L.** (Martyniaceae): An annual that normally flowers during July-October. Flowers open everyday between 0400-0500 hrs. The flowers are large, showy, bisexual and nectariferous. The corolla is pendant and tubular, with its mouth containing nectar guides directed laterally. The stamens are epipetalous, with syngenecious anthers. The style with bilobed stigma overarches the anther. Flowers are foraged by carpenter bees, digger bees and hawkmoths during the day. The hawkmoth is an inefficient pollinator, but may compel the bees to make multiple visits to the flowers by depleting nectar. The two bee species are equally efficient in pollination of the taxon. While probing the flowers, they land on the large lip and penetrate into the corolla tube following the nectar guides. In doing so, their dorsal side touches the sex organs and pollination results.

15. ***Moringa oleifera* Lam.** (Moringaceae): Popularly known as the drumstick tree, it thrives best under a tropical insular climate. The tree is valued for the tender pods used as vegetables. This tree blooms twice a year, during February-May and again during September-November; the former blooming is more intense. The flowers open between 0500-0900 hrs. They are creamy white, large, showy, bisexual and nectariferous. They are foraged by a variety of insects but carpenter bees and digger bees are the main pollinators. Even among these, carpenter bees are the most appropriate for manipulating the flower. Carpenter bees gather only nectar; while doing so, they alight on the reflexed petals and probe for nectar during which the sex organs brush against their dorsal side, effecting nototriby. They travel long distances to forage on widely dispersed conspecific plants. This inter-tree movement promotes xenogamy. The bees are also opportunistic in that they use other nectariferous plants in the study area.

Discussion and Conclusions

Most of the plant species described are zygomorphic, large, showy and bisexual; some have long tubes and others short, all perfectly adapted to pollination by carpenter bees. Species with the sex organs placed near or along the upper lip are adapted to nototriby. *Caesalpinia* and *Gliricidia* have their sex organs in the lower part of the corolla and are adapted to sternotriby. The anthesis timings in different plant species are different, some at night, others during the day and one, i.e. *Alangium*, both day and night; but the flowers of all the species are foraged diurnally. *Anisomeles* and *Acanthus* are foraged by insects as well as sunbirds. *Caesalpinia* and *Cassia* are outcrossers, exclusively foraged and pollinated by carpenter bees. Some plant species are foraged by different groups of insects and others exclusively by bees, but carpenter bees are the main pollinators, also *Amegilla* for *Martynia* and sunbirds for *Acanthus* and *Anisomeles*. Carpenter bees effect pollination through nototriby and sternotriby; the former is a more advanced mechanism in which pollen deposition is very precise and not accessible for grooming by the bees. It ensures pollination success, while in sternotriby, pollen wastage takes place during grooming of the bee and in flight, and is thus not economical.

Carpenter bees exhibit buzzing behaviour while collecting pollen of the nectarless *Cassia* and *Cochlospermum,* in which anther dehiscence is poricidal, and of *Peltophorum* flowers with

longitudinally dehiscent anthers. Buzzing is typical in pollinators of poricidal flowers that exhibit heteranthery and enantiostyly as in *Cassia,* or without these devices as in *Cochlospermum* (Buchmann 1983), while *Peltophorum* with firmly adhered oily pollen is also buzz-pollinated. On some plant species, the carpenter bees exhibit territoriality or traplining or both, and on others, opportunistic foraging behaviour. Territoriality means that the bees select a population of flowers rich in nutrients, usually from one plant species, and obtain food within the same population throughout the flowering season. When exhibiting territorial behaviour, male bees alternately defend the selected flower population by chasing away intruders and forage on the flowers. Traplining is a foraging behaviour in which bees make long distance flights and remember images of the whole region visited on their regular rounds. Opportunistic behaviour is when the bees exploit floral resources, mainly nectar, from the flowers of various plant species co-occurring and blooming simultaneously, in order to obtain forage for themselves and for their offspring (Pijil 1954, Janzen 1964, Frankie 1976, Barrows 1980, Frankie *et al.* 1983, Aluri and Subba Reddi 1989). Of these types of behaviour, territoriality and traplining impose fidelity in bees to remain faithful to one flowering plant species, greatly promoting outcrossing, whereas opportunistic behaviour facilitates the use of available flowering species in the biotope, depending on the floral density or intensity of flowering.

All the plant species except *Cassia*, *Cochlospermum* and *Couroupita* are nectariferous, with nectar volumes ranging from 0.8 to 80 µl and sugar concentrations from 5 to 48% (authors' data). The foraging of carpenter bees on these plant species indicates that they make use of variously concentrated sugars as available at different times of the year for their sustenance. Nectarless plant species provide pollen rich in nutrients to carpenter bees. The floral structural and functional devices, coupled with variously coloured corolla: yellow, purple, creamy-white, sometimes lavender, are evolved for foraging by carpenter bees exclusively or preferentially.

Both plants and carpenter bees mutually benefit each other, and thereby ensure perpetuation of both in their respective biotopes. There is unequivocal evidence of the importance of carpenter bees in the reproduction of different species of plants, and thus for the production of plant biomass of terrestrial ecosystems, and for generating and maintaining genetic diversity of the plants.

References

Aluri, J.S.R. (1990): Observations on the floral biology of certain mangroves. *Proc. Indian Nat. Sci. Acad. (B)56*: 367-374.

Aluri, J.S.R. (1993): Ecology of pollination and reproduction in *Couroupita guianensis* Aubl. (Lecythidaceae). *J. Nat. Conserv. 5*: 47-52.

Aluri, J.S.R.. & C. Subba Reddi (1989): Pollination biology of *Anisomeles indica* and *A. malabarica* (Lamiaceae). *Pl. Sp. Biol. 4*: 157-167.

Aluri, J.S.R.. & C. Subba Reddi (1994): Observations on pollination in *Alangium salviifolium* (Linn.f) Wang. (Alangiaceae). *J. Bombay nat. Hist. Soc. 91(2)*: 345-347.

Aluri, J.S.R. & C. Subba Reddi (1996a): Vibrational pollination in *Peltophorum pterocarpum* (Caesalpiniaceae). *J. Nat. Conserv. 8*: 99-100.

Aluri, J.S.R.. & C. Subba Reddi. (1996b): Floral biology and pollination in *Gliricidia sepium* (Fabaceae) *J. Nat. Conserv. 8*: 65-67.

Barrows, E.M. (1980): Robbing of exotic plants by introduced carpenter bees and honey bees in Hawaii, with comparative notes. *Biotropica 12*: 23-29.

Bhaskara Rao, C. & C. Subba Reddi (1994a): Pollination ecology of *Martynia annua* L. *J. Bombay nat. Hist. Soc. 91(2)*: 187-193.

Bhaskara Rao, C. & C. Subba Reddi (1994b): Reproductive biology of *Cochlospermum religiosum. J. Trop. Ecol. 35*: 209-218.

Buchmann, S.L. (1983): Buzz-pollination in angiosperms. *In*: Handbook of Experimental Pollination Biology.

Eds.: C.E. Jones and R.J. Little, Scientific and Academic Editions, New York, pp. 73-13.

CHAPPEL, M.A. (1982): Temperature regulation of carpenter bees (*Xylocopa californica*) foraging in the Colorado desert of Southern California. *Phys. Z. 55*: 267-280.

FRANKIE, G.W. (1976): Pollination of widely dispersed trees by animals in Central America, with an emphasis on bee-pollination systems. *In*: Tropical Trees: Variation, Breeding and Conservation. Eds.: J. Burley and B.T. Styles, Academic Press, London, pp. 151-159.

FRANKIE, G.W., W.A. HABER, P.A. OPLER & K.S. BAWA (1983): Characteristics and organisation of the large bee-pollination system in the Costa Rican dry forest. *In*: Handbook of Experimental Pollination Biology. Eds.: C.E. Jones and R.J. Little, Scientific and Academic Editions, New York, pp. 411-447.

JANZEN, D.H. (1964): Notes on the behaviour of flower subspecies of the carpenter bee *Xylocopa* (*Notoxylocopa*) *tabaniformia* in Mexico. *Ann. Entomol. Soc. Am. 57*: 296-301.

JYOTHI, P.V., ATLURI, J.B. & C. SUBBA REDDI (1990): Pollination ecology of *Moringa oleifera* (Moringaceae). *Proc. Indian Acad. Sci. (Plant Sci.) 100*: 33-42.

MAXWELL-LEFROY, H. & F.M. HOWLETT: (1971): Indian Insect Life, A manual of the Insects of the plains (Tropical India). Today and Tomorrow's Printers and Publishers, New Delhi.

PIJL, L. VAN DER (1954): *Xylocopa* and flowers of the Tropics 1. The bees as pollinators: Lists of the flowers visited. *Proc. Koninkl. Nederl. Akad. Van. Wetenschappen (Amsterdam) Series C 57*: 413-423.

SCOTT, P.E., L. STEPHEN, S.L. BUCHMANN & M.K. O'ROURKE (1993): Evidence for mutualism between a pollen-piercing carpenter bee and Ocotillo : Use of pollen and nectar by nesting bees. *Ecol. Entomol. 18*: 234-240.

SNOW, A.A. & D.W. ROUBIK (1987): Pollen deposition and removal by bees visiting two tree species in Panama. *Biotropica 19*: 57-63.

SUBBA REDDI, C. & J.S.R. ALURI (1997): Reproductive biology of three mangrove plant species. *Indian J. Forestry 20*: 153-157.

SUBBA REDDI, C. & C. BHASKARA RAO (1993): Pollination ecology of *Bauhinia purpurea* (Caesalpiniaceae.) *J. Palynol. 29*: 115-124.

SUBBA REDDI, C., K. RAMA DAS, J.S.R. ALURI & J.B. ATLURI (1996): Sexual system and pollination ecology of *Gmelina asiatica* L. (Verbenaceae). *J. Palynol. 32*: 41-50.

SUBBA REDDI, C., J.S.R. ALURI, J.B. ATLURI & C. BHASKARA RAO (1997): Enantiostyly, heteranthery and carpenter bee pollination in *Cassia alata* L. (Caesalpiniaceae). *J. Palynol. 33*: 149-152.

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